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Mechanics of One- and Two-Joint Muscles

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INTRODUCTION

The recent surge of interest in evolutionary morphology has forced morphologists to re-evaluate older methods and, when necessary, to develop new methods for the analysis of forces in bone-muscle systems. Considerable success has been attained in studies of the skeletal system which has proved to be amenable to a variety of approaches (Pauwels, 1965; Evans, 1957; Kummer, 1959a, 1959b, 1961, 1966). Frazzetta (1962, 1966, MS) has, for example, employed a number of methods from machine theory (kinematics) to analyze the movements of individual skeletal units in the complex bone systems of the reptilian skull. Investigations of the muscular system have enjoyed considerably less success. Excellent methods have existed for many years for the treatment of forces in the movements of entire limbs or of segments of limbs; these forces can then be compared with estimates of the total force developed by the muscular system (Fenn, 1930a, 1930b, 1938; Elftman, 1939a, 1939b, 1940, 1941, 1966; Manter, 1938). Unfortunately these methods do not permit treatment of the force produced by a single muscle or by various combinations of individual muscles. Clear and practical methods are not readily available to the morphologist for the analysis of the force developed by individual muscles functioning normally within bone-muscle systems. None of the several methods advocated previously have been

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adopted widely, suggesting that the practical difficulties encountered in their application to actual cases outweigh their advantages. Nevertheless, the continued prevalence of vague and often misleading conclusions on the functional properties of individual muscles in recent comparative and phylogenetic morphological studies of vertebrate muscle-bone systems indicates the need for a simple (as possible) and practical method of analysis.

The goal of this paper is to present a general method for the investigation of the forces produced by one-joint and two-joint vertebrate skeletal muscles based on the concept of free-body diagrams (see any text on mechanics, e.g., Den Hartog, 1961; Dempster, 1961; Dempster and Duddles, 1964). The level of analysis is the bone-muscle system. The exact structure of the muscle and its functional properties (Gans and Bock, 1965) are of no importance to this study; only the muscle force and its direction are included in the analysis. The force of each muscle is treated as a single force vector, which may be a simplification in some cases. I wish to emphasize at the outset that the approach to be developed does not and cannot solve all the problems in the study of muscle function. Questions such as maximum force development and variation in force during contraction lie completely outside the method of free-body diagrams.

ONE- AND TWO-JOINT MUSCLES

The major morphological distinction in this study is between one-joint and two-joint skeletal muscles regardless of the size and of the fiber arrangement of the muscles. One-joint muscles are those that run from one bone to the next successive bone, and thus pass over only one articulation (fig. 1A). Two-joint muscles are those that run from one bone, bypass the next successive bone and attach onto the third bone of the series, and therefore pass over two articulations (fig. 1B). Most one- and two-joint muscles in the same limb segment are similar in their length and in their sites of attachment, because one-joint muscles usually originate close to the proximal end of the bone, and two-joint muscles generally originate just across the articulation on the distal end of the next more proximal bone; the insertions of these muscles are usually close together. Moreover, some muscles, e.g., M. triceps, have two heads of origin, one on each side of an articulation; hence part of the muscle is a one-joint, and part is a two-joint, muscle. Only those muscles having a direct straight pull from their origin to their insertion are considered, i.e., those in which the force lies along a single vector line that connects the points of origin and insertion. Complications exist in the analysis of muscles in which the

tendon bends around a collagenous-fibered loop or pulley, or in which the tendon curves around an articulation and is bound closely to the bone by a tendon sheath. Most muscles that pass over more than two joints are of the latter type. Some multi-joint muscles, such as cervical muscles in long-necked birds, are exceptions, but these are also difficult to analyze because the movements of the skeletal elements may not be determinate.

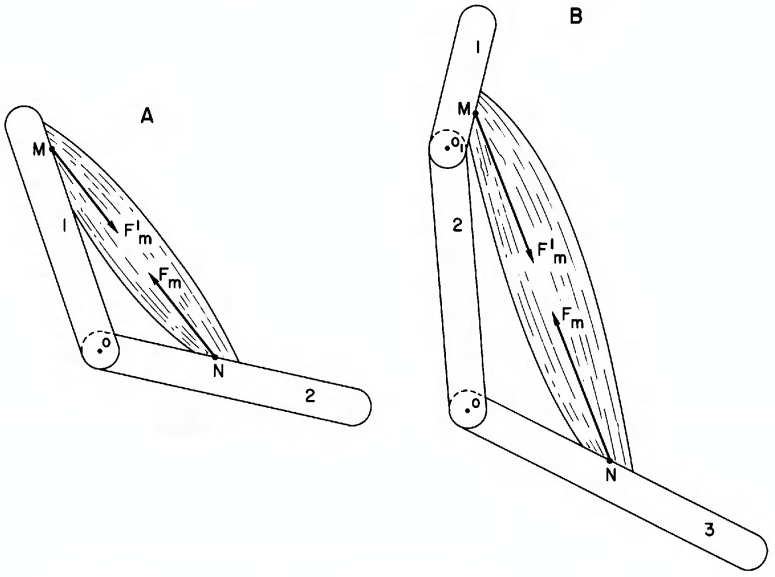

FIG. 1. Schematic drawings of two simple flexor muscles, to show the relationship between the muscle, the force vectors of the muscle (F_m and F'_m), and the bones. A. One-joint muscle. B. Two-joint muscle.

An extensive literature on two-joint muscles exists (Baeyer, 1921; Basmajian, 1957, 1962; Bois-Reymond, 1903; Fenn, 1938; A. E. Fick, 1879; R. Fick, 1910; Fisher, 1906; Manter, 1938; Rasch and Burke, 1963; Strasser, 1908), most of it dealing with human muscles and much of it based on experimental studies, yet few of the results and conclusions of these studies have been utilized in general vertebrate functional morphology. Many properties of two-joint muscles as well as their advantages and disadvantages compared to one-joint muscles have been suggested in these papers. A discussion of these properties and comparisons with one-joint muscles can be done best after the method for analyzing the forces of these muscles is outlined.

THE METHOD OF FREE-BODY DIAGRAMS

The basic analysis employed is the method of free-body diagrams (Dempster, 1961; Bock, 1966; Williams and Lissner, 1962; and any general college-level textbook of mechanics or physics; the term "free-body diagram" may not, however, appear in a physics text). Free-body diagrams are a most useful approach in studies of bone-muscle systems in that all forces acting on a single structural element must be accounted for in the analysis (see Dempster, 1961, for historical background and a detailed discussion of this approach). This method has been employed primarily for studies of forces on skeletal elements, but rarely, if ever, for study of muscle forces and their consequences. The only requirement demanded for the use of free-body diagrams is that all external forces acting on the body be included in the analysis. For the purposes of this study, I make several simplifying assumptions and restrictions to reduce the complications of the biological systems to rather ideal physical ones. Most of these simplifications are similar to those frequently applied by engineers in the analysis of complex real systems. It must be emphasized that calculations based on free-body diagrams applied to actual cases of bone-muscle systems will be approximations rather than exact answers; experimental observations are required to ascertain the actual forces existing at different points in the system and to justify the simplifying assumptions.

The assumptions used in this study are: (a) that the skeletal elements are rigid bodies; (b) that no friction or other force-absorbing processes occur at the points where external forces act on the skeletal elements; and (c) that the articulations are ideal joints which are frictionless and do not store energy that may be released later. Most, but not all, vertebrate bones that can be analyzed with the help of free-body diagrams are quite rigid under the loads usually applied. Those bones that deform (e.g., bend, as is the case of the upper jaw in many birds) under the forces usually applied to them cannot be treated with the equations herein developed. Nevertheless, these flexible bones can still be handled by free-body diagrams. Friction at the point of force application may impose a serious problem that must be resolved in some actual studies, but it has been ignored in this treatment. Friction probably cannot be ignored when one or more of the forces are external to the animal, such as the force of a foot against the ground. Articulations between bones may also present considerable problems. The articular surfaces in diarthroses are generally quite frictionless, but the amount of energy absorbed or stored, or both, by the collagenous-fibered capsule and articular ligaments may be considerable under certain conditions. Synarthroses and other forms or

articulations may have rougher surfaces and higher coefficients of friction. Other articulations, such as the nasal-frontal hinge in many birds, consist of a flexible sheet of bone, the bending of which requires force. In all cases, the loss or storage of energy at the articulation must be determined by empirical observations.

In all cases, the center of rotation of the skeletal elements is at the articulation, and this center of rotation is a line at right angles to the

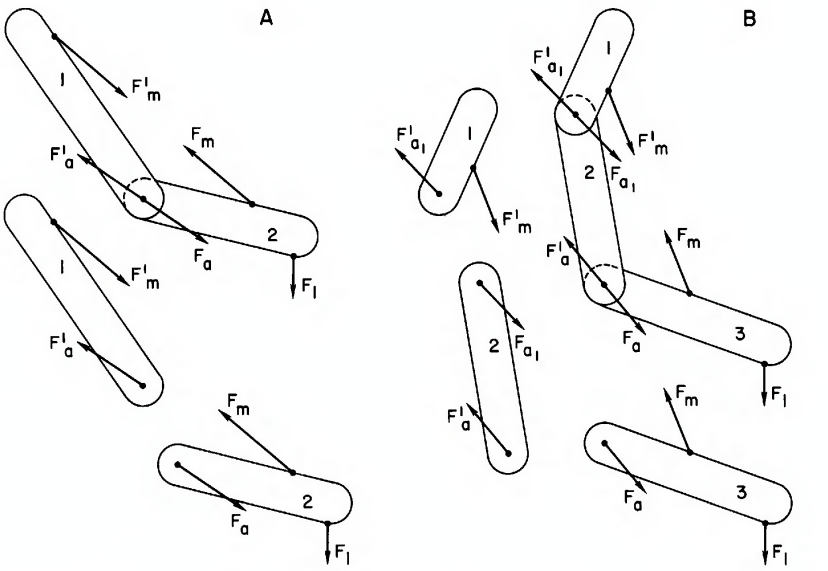

FIG. 2. Schematic drawings and free-body diagrams of two simple flexor muscles, following figure 1 but including the force at the articulation (F_a) and a load force (F_l) on the distal bone. A. One-joint muscle. B. Two-joint muscle. Note that a free-body drawing is drawn for each bone and that all external forces on each bone are shown.

plane of motion and hence appears on the figures as a point. The articulation is regarded as an ideal hinge. Other requirements are that the points of application and direction of the force vectors are known exactly, that the centers of gravity and masses of the free-bodies are known, and that the moments of inertia (always about the articulation) of these bodies are known. Again these requirements may not be met precisely in actual studies, but they can generally be approximated closely. The necessity of making a number of assumptions should not be discouraging, because the disadvantages of a partly artificial or simplified system are greatly outweighed by the advantages afforded by free-body diagrams both as a theoretical approach and as a rich source of working hypothe-

ses for further testing in functional anatomical studies of bone-muscle systems.

One important aspect of free-body diagrams is that one body must be analyzed at a time and if possible drawn separately. Only the external forces acting on that body should be shown. The several free-body diagrams for a simple one-joint muscle and a simple two-joint muscle are shown in figure 2. In this study I have assumed that the bone from which the muscle takes origin is stationary and have not drawn a free-body diagram for it. This bone and the muscle force acting on it have been shown by dashed lines for reference in some of the free-body diagrams; however, I must emphasize that any bodies or forces indicated by dashed lines are not part of the free-body diagram shown in each figure.

The lengths of the arrows have not been drawn proportional to the magnitude of the forces, as is conventional, because I was concerned only with the development of general methods, and numerical values were not assigned to any of the forces. Except where noted, all forces are considered to be coplanar and in the plane in which the bones move. In all cases, the center of the rectilinear coordinates was placed at the center of rotation. All forces were decomposed into their rectilinear components and then added. These forces can also be added directly with the use of methods of vector summation such as the simple polygon method.

Free-body diagrams may be used in both static and dynamic studies. In dynamic cases, the moving bone may be rotating about an axis (line) through the center of rotation, or may be moving in a rectilinear direction, or a combination of both. In the last case the movement of the bone can be analyzed with respect to the instant center of rotation, as was done by Frazzetta (1966, MS). I have treated all dynamic conditions as instantaneous conditions as shown in the diagram; no attempt has been made to solve the equations for dynamic cases over the range of movement. In actual studies these equations would have to be solved exactly by integration (which will be very difficult in most cases) or approximately by dividing the range of movement into a series of steps. The latter method will probably be sufficiently accurate when compared with the accuracy of the observations and measurements of the forces, moment arms, and the various simplifying assumptions.

I wish to emphasize that the method of free-body diagrams as used in this study is little more than simple lever analysis. It does differ from most lever analyses in that all the forces acting on the structural element are included; the forces at the fulcrum are frequently omitted in the lever analyses used in functional anatomical investigations. Moreover, there is no need to divide the possible lever systems into a classification

of first-, second-, and third-class levers depending on the arrangement of the forces relative to the fulcrum. Nothing is gained by such a classification of levers that could not be shown as well or better by free-body diagrams. Indeed, the division of levers into several classes frequently leads to the erroneous impression that each class of lever possesses different and distinct properties, for example, that first- and third-class levers provide increased speed at the sacrifice of force, whereas second-

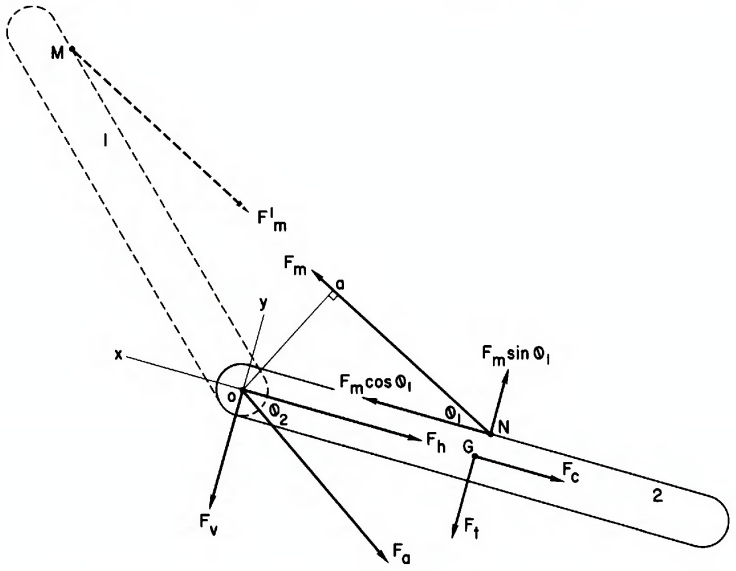

FIG. 3. Schematic drawing of a one-joint flexor muscle and free-body diagram of bone 2 onto which the muscle inserts. All structures and forces shown by dashed lines are not part of the free-body diagram. The system is under gravity-free conditions. See text for further explanation.

class levers sacrifice speed for increased force (see Rasch and Burke, 1963, pp. 155–156). Because the use of first-, second-, and third-class levers requires the memorization of additional and rather unnecessary factual information, I recommend strongly that this usage be abandoned in favor of the simpler method of free-body diagrams.

ONE-JOINT MUSCLES

A simple one-joint flexor muscle, such as the brachioradialis in man, is shown in figure 3, with the muscle originating from bone 1 at point M and inserting on bone 2 at point N. In this and all other examples in this study, the mass of the muscle has been ignored. When the muscle con-

tracts, it exerts an equal and opposite tensile force F_m and F'_m on both bones; the consequences of this force depend on all the other forces acting on the bones. Bone 1 is regarded as fixed in position, whereas bone 2 is free to move (e.g., to rotate). A more general analysis is possible, if both bones were allowed to move. However, holding one bone fixed simplifies the analysis greatly without reducing its general applications or affecting the conclusions on the properties of one-joint or two-joint muscles. I should point out that, in many cases among vertebrates, such as fish swimming or birds flying, no part of the body may be considered to be fixed in position, and the relative movement of each part of the body must be ascertained. The two bones articulate in an ideal pinlike joint at point o which allows free rotation of bone 2. For certain analyses, the structure of the joint has been considered to be so modified as to allow linear movement of bone 2 past bone 1. In all cases, the masses of the moving bones are included in the analysis. Free-body diagrams and equations are formulated only for bone 2.

The Gravity-free Condition: In the first case (fig. 3), the force of gravity has been excluded, although I realize that such a condition was artificial for all vertebrates until quite recently when several species of vertebrates, including man, were orbited around the earth in a space capsule and were placed in a prolonged free-fall, an essentially gravity-free environment. The force relationships within muscle-bone systems under gravity-free conditions are quite interesting for a fuller understanding of muscle mechanics and deserve special treatment. Because this condition permits a clear comprehension of the influence of non-muscular forces on the consequence of the muscular force, it is considered first.

The force vector F_m of the muscle acts on bone 2 at point N. Because this force does not pass through the center of rotation, o, of bone 2, it imparts a rotational effect on this bone. The rotational effect of this force can be completely described by the following three equation (considering only the instantaneous condition shown in figure 3 in which the x-axis coincides with the longitudinal axis of bone 2):

$$\Sigma M_o = I_o\alpha; \text{ and} \quad (1)$$
$$\Sigma F_x = ma_x = m\omega^2 R_G; \text{ and} \quad (2)$$
$$\Sigma F_y = ma_y = m\alpha R_G. \quad (3)$$

Equation 1 is the sum of the moments or torques acting on the bone, in which I_o is the moment of inertia of the bone about o and α is the angular acceleration. Equation 2 is the summation of forces in the x direction, in which a_x is the radial acceleration, hence $m\omega^2 R_G$ is the centripetal force. Equation 3 is the summation of forces in the y direction, in which

a_y is the tangential acceleration, hence $m\alpha R_G$ is the tangential force.[1] The term ω is the angular velocity of the bone, and the term R_G is the radius of the center of gravity from the center of rotation o. Throughout this paper, all equations are written in the form of d'Alembert's principle, hence the terms $I_o\alpha$, $m\omega^2R_G$, and $m\alpha R_G$ are fictitious "inertia torques" or "inertia forces" (see below). The fictitious "inertia forces," $m\omega^2R_G$ and $m\alpha R_G$, act on the body as if the entire mass of the body were concentrated at its center of gravity. The two terms, $m\omega^2R_G$ and $m\alpha R_G$, may be considered as the centripetal and tangential inertia forces that are directed against the acceleration of the free-body. The term $I_o\alpha$ may, likewise, be considered as an "inertia torque" directed against the angular acceleration of the body. These equations and the forces involved are discussed in detail in the following paragraphs.

In the first example, as shown in figure 3, the vector of the muscle force, F_m, does not pass through the center of rotation, o, of bone 2, hence exerts a torque (or moment) on this bone; the torque is the product of the force and the moment arm of the force. The moment arm, oa, of the force vector F_m is obtained by dropping the perpendicular from the center of rotation to the line of the force vector. The magnitude of the torque (or moment) becomes greater with an increase in either the force or its moment arm, or both. In this simplest case, the muscle force is the only torque-producing force acting on bone 2. The sum of moments (torques; clockwise[2] torques are positive) on bone 2 is:

$$\Sigma M_o = -F_m(oa) = -I_o\alpha. \tag{4}$$

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[1] An excellent statement describing the factors acting in the rotation of a flat body about a fixed axis can be found in Den Hartog (1961, p. 233) and is here quoted in full: "The angular acceleration $\dot{\omega}$ $[=\alpha]$ of a thin, flat, rigid body constrained to move in rotation about a fixed axis 0 perpendicular to its plane is found from the formula:

$$\text{Moment of external forces about } 0 = I_o\dot{\omega}$$

while the reaction forces from the axis on the body are determined by solving the static equilibrium equations of the body under the influence of the external forces and of two fictitious 'inertia forces' $m\dot{\omega}r_G$ and $m\omega^2r_G$, as if the entire mass of the body were concentrated at its center of gravity." This statement sums up the entire physical basis for the analysis in the present paper.

[2] By clockwise torque, I mean a force-lever arm combination that tends to rotate the bone in a clockwise direction; counterclockwise torques tend to rotate the bone in the opposite direction and are designated as negative in sign. In a like fashion, the sign used for the $I\alpha$ term designates the direction of rotation, with clockwise rotation being positive. The sign of the fictitious inertia torque term is, therefore, opposite to the direction of rotation and would be negative for clockwise rotation. The positive or negative signs of the $I\alpha$ term will not designate acceleration or deceleration, as is another common convention.

Hence the bone will rotate in a counterclockwise direction, with the angular acceleration (α) depending on the moment of inertia (I_o) of the bone for a fixed force produced by the muscle. The sum of the moments may be rewritten, in the form of d'Alembert's principle, as:

$$\Sigma M_o = -F_m(oa) + I_o\alpha = 0. \quad (5)$$

The term $I_o\alpha$ in this equation is the fictitious torque (or inertial torque) of bone 2, equal in magnitude but oppositely directed to the $I_o\alpha$ term in equation 4. D'Alembert's principle has been used throughout this study as a means of reducing all dynamic situations to equilibriums which can then be treated with the methods of statics. Because the moment of inertia of a bone (or limb segment, or jaw) generally remains constant, the speed at which the bone will rotate depends on its angular acceleration (and the duration of the acceleration), and its angular acceleration depends on the magnitude of torque resulting from the muscle force. Any increase in torque, either by increase in the magnitude of the force or by length of the moment arm or by a combination of both, will increase the angular acceleration and hence the speed of rotation of the bone.

In addition to providing the torque for angular acceleration, the tensile force developed by the muscle provides some or all of the centripetal and tangential forces needed for acceleration in these directions. The centripetal force acts along the longitudinal axis of bone 2 toward the center of rotation; it appears in the figures and equations as the fictitious centripetal force or centrifugal inertia force acting away from the center of rotation. For a bone of fixed center of gravity and constant mass, the centripetal force depends on the angular velocity (proportional to the square of the angular velocity). The centripetal force remains the same for constant angular velocity but would increase as the velocity increases (i.e., under conditions of angular acceleration). Whenever one bone rotates, it is generally being accelerated (or decelerated) while it moves; hence the centripetal force will always vary and is time dependent. Rarely does a bone rotate at constant angular velocity, hence rarely are the radial acceleration and the centripetal force constant. Because of the stress placed on the bones and on the articulation, the maximum centripetal force may be of the greatest interest. It should be pointed out that the muscle force may provide only part of the needed centripetal force. Some, or even all, of the centripetal force component may be provided by the resistance of the articular ligaments to the centrifugal force of the rotating bone. This point is discussed in detail below (p. 22).

The tangential force acts at right angles to the longitudinal axis of bone 2 in the direction of rotation of the bone; again it appears in the figures and equations as the fictitious tangential force or tangential in-

ertia force acting opposite to the tangential acceleration of the bone (i.e., in direction, this inertia force is directed opposite to the direction of rotation of the bone). This force may be thought of as the tangential inertia force that must be overcome before the bone will accelerate or as the tangential force acting at the center of gravity of the bone needed to produce the same angular acceleration as would force F_m acting at point N. A tangential force (inertia force) must be considered only if the bone is undergoing angular acceleration. When the bone is rotating at constant angular velocity, no tangential force exists. Unlike centripetal force, which varies with increasing angular velocity or with time under conditions of constant angular acceleration, tangential force remains constant with constant acceleration and does not vary with time. The needed tangential force is produced only by the muscle force (in this case) and other torque-yielding forces. It cannot be provided by resistance of articular ligaments as in the case of centripetal force (see below, p. 23, for a full discussion).

In addition to its rotary effects on bone 2, the tensile force developed by the muscle acts to pull bone 2 against bone 1. This effect appears as a force acting at the articulation of the two bones and can be analyzed by some form of vector addition. The easiest and clearest method is to decompose all forces into rectangular components. A set of x-y axes must first be drawn through the center of rotation. The orientation of these axes depends only on the choice of the worker, and they are usually so placed for the greatest convenience and utility to the particular study. In studies of static conditions, it is often useful to place one axis parallel to the longitudial axis of the fixed bone so that one of the component forces at the articulation will appear as compression or tension on this bone. However, in conditions of rotational movement, it is usually best to place one axis along the longitudinal axis of the moving bone so that the centripetal force is parallel to one axis and the tangential force is parallel to the other axis. In this case, the x-y axes were placed so that the x-axis is parallel to the longitudinal axis of bone 2 which allows an easy summation of forces.

The force F_a at the articulation is the force exerted by bone 1 on bone 2; it is equal and opposite to the force F'_a exerted by bone 2 on bone 1 which depends on all other forces, real and fictitious, acting on bone 2. This force passes through the center of rotation, hence does not exert any torque on bone 2. Because the magnitude and vector direction of the force F_a are generally not known until after the several equations are solved, it is often more convenient to show its two component forces, F_h and F_v, rather than the force itself.

Once the x-y axes are chosen, each force can be decomposed into its component forces. Force vector F_m intersects the x-axis at angle θ_1; hence its component forces are $F_m \cos \theta_1$, along the x-axis and $F_m \sin \theta_1$ along the y-axis. The articular force, F_a, is represented by F_h ($= F_a \cos \theta_2$) along the (horizontal) x-axis and F_v ($= F_a \sin \theta_2$) along the (vertical) y-axis. The centripetal (F_c) and tangential (F_t) inertia forces must be included. The forces acting along the x-y axes can be added algebraically (with forces acting toward the right along the x-axis and upward along the y-axis being positive). Thus if the two bones are in static equilibrium along the x-y axes, then:

$$\Sigma F_x = -F_m \cos \theta_1 + F_h + F_c = 0; \text{ and} \quad (6)$$
$$\Sigma F_y = F_m \sin \theta_1 - F_v - F_t = 0. \quad (7)$$

The centripetal inertia is equal to $m\omega^2 R_G$ and increases as the angular velocity increases, whereas the tangential inertia is equal to $m\alpha R_G$ and is constant with constant angular acceleration. If bone 2 is moving past bone 1 in some linear direction, then it is undergoing a linear acceleration in addition to the accelerations associated with the rotational movement.[1] The equations can then be written, with the use of the form of d'Alembert's principle as:

$$\Sigma F_x = -F_m \cos \theta_1 + F_h + F_c + ma_x = 0; \text{ or} \quad (8)$$
$$\Sigma F_y = F_m \sin \theta_1 - F_v - F_t - ma_y = 0, \text{ or both,} \quad (9)$$

in which m is the mass of bone 2 and a_x is the linear acceleration along the x-axis and a_y is the linear acceleration along the y-axis; the signs of the ma terms are directional only, depending on the direction of the inertia force. The actual linear acceleration of bone 2 is the result of the accelerations along the x and the y axes. The proper combination of these formulas must be chosen according to the existing conditions.

In the construction of figure 3, bone 2 was allowed to rotate only and was not allowed to slide past bone 1—this being the simplest rotational movement that can be described by equations 5, 6, and 7. Under these conditions, force F_h is equal to $F_m \cos \theta_1 - F_c$, and force F_v is equal to $F_m \sin \theta_1 - F_t$. The resultant vector F_a of the forces F_h and F_v is the force exerted by bone 1 onto bone 2 at their articulation. Because of the presence of the centripetal and tangential inertias when bone 2 is under angular acceleration, the force F_a is always different (usually less) from F_m, and the vector directions of these forces are not parallel. Hence,

[1] If bone 2 is moving past bone 1 in some linear direction, then its moment of inertia, I_o, and the distance between the center of rotation and the center of gravity, R_G, would be changing. However, these changes can be ignored in most cases, because bones undergo very limited linear movement past one another.

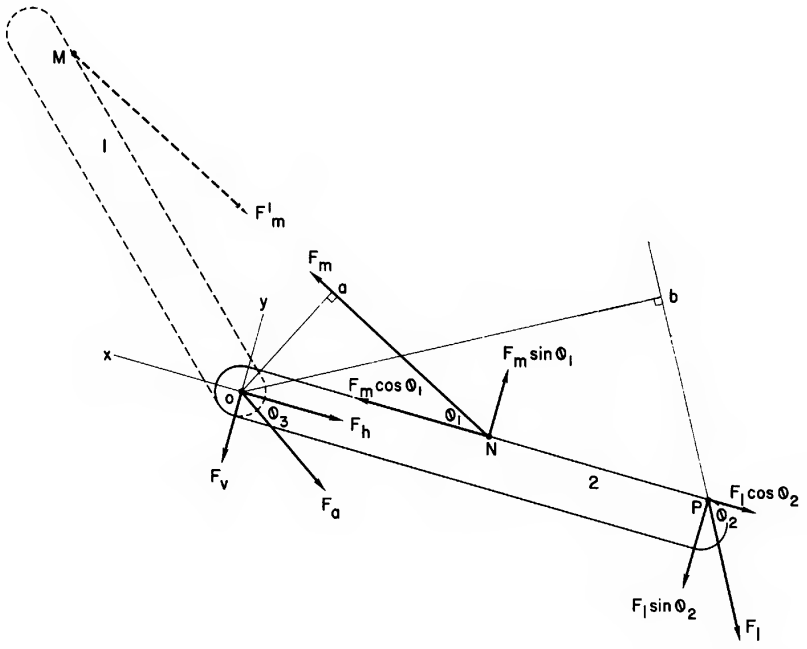

FIG. 4. Schematic drawing of a one-joint flexor muscle and free-body diagram of bone 2. The system is the same as in figure 3 except for the addition of a load force (F_1). See text for further explanation.

forces F_m and F_a can never constitute a force couple[1] acting on bone 2 (see below, p. 33, for a discussion of this important point.)

In the second example under gravity-free conditions, static equilibrium, both rotational and linear, exists when a second force, F_1, acting on bone 2 opposes the force developed by the muscle (fig. 4) so that the sums of the moments and of the vector forces are equal to zero, thus:

$$\Sigma M_o = -F_m(oa) + F_1(ob) = 0; \text{ and} \qquad (10)$$

[1]The term "force couple" or "couple" throughout this paper designates a simple force couple, i.e., a pair of parallel forces, equal in magnitude, but acting in opposite directions. It is never used in the meaning of a turning couple. The term "couple" in the biomechanical literature, e.g., "The total effect of the action of a one-joint muscle can be most simply represented by two equal and opposite couples, one on each of the adjacent members on which the muscle acts" (Manton, 1938, p. 535), has always been used in the sense of a simple force couple, although the term "turning couple" is frequently used (e.g., Gray, 1956, p. 203). No clear definition has been given, to my knowledge, for "turning couple," nor has this term been distinguished from force couple in the biomechanical literature. The German term "Kraftpaar" translates directly as force couple.

$$\Sigma F_x = -F_m \cos \theta_1 + F_1 \cos \theta_2 + F_h = 0; \text{ and} \quad (11)$$
$$\Sigma F_y = F_m \sin \theta_1 - F_1 \sin \theta_2 - F_v = 0. \quad (12)$$

Note that the $I_o\alpha$, F_c, and F_t terms are absent, because bone 2 is not undergoing angular acceleration. The terms ma_x and ma_y are missing, because bone 2 is not undergoing linear acceleration. In this case, because of the vector direction of force F_1, its x and y components cancel out much of the x and y components of force F_m so that the resultant force at the articulation is reduced. However, when force F_1 acts along certain other vector directions, its components may add to the components of force F_m and increase the total force on the articulation. Tensile forces at the articulation are resisted by the collagenous fibers of the articular capsule and associated ligaments, while compression forces are resisted by the cartilage and bone.

In this example, when bone 2 is under static conditions, a second force, F_1, must always act upon the bone. Because force F_1 is present and must be added vectorially to force F_m for one to ascertain the magnitude and direction of the force at the articulation, F_a, the force vectors F_m and F_a can never constitute a force couple acting on bone 2 (see below, p. 33, for additional discussion).

THE GENERAL CASE: A general statement describing the mechanics of a simple one-joint (flexor) muscle can be made with the aid of figure 5. The arrangement of the muscle and bones is the same as in figures 3 and 4. The major difference between the present case and the cases discussed above is that the force of gravity is included and is shown as the force F_g acting at the center of gravity, G, of bone 2. Because bone 1 is fixed, the pull of gravity on this structure does not affect the bone-muscle system under consideration. A second force, F_1, acts on bone 2 at point P.

Several possible static and dynamic conditions are analyzed, with the use of the same conventions as above. No attempt was made to include all possible conditions, which would be overly repetitious. In all cases, the conditions are stated explicitly.

When bone 2 is under static conditions, then the sums of the moments and of the vector forces are equal to zero; hence

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) = 0; \text{ and} \quad (13)$$
$$\Sigma F_x = -F_m \cos \theta_1 + F_g \cos \theta_2 - F_1 \cos \theta_3 + F_h = 0; \text{ and} \quad (14)$$
$$\Sigma F_y = F_m \sin \theta_1 - F_g \sin \theta_2 - F_1 \sin \theta_3 - F_v = 0. \quad (15)$$

The direction of the F_h and F_v forces and of their resultant force, F_a, can be determined only after the other forces are calculated and added.

When bone 2 is undergoing angular acceleration, i.e., rotating under the action of the muscular force, then the equations are as follows:

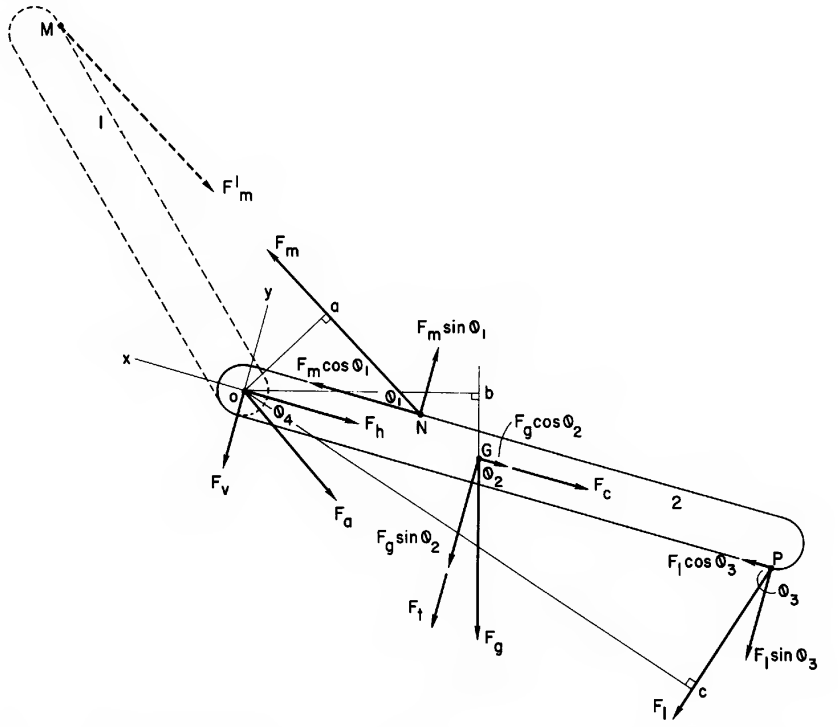

FIG. 5. Schematic drawing of a one-joint flexor muscle and free-body diagram of bone 2. The system is the same as in figures 3 and 4 except that it is under gravity conditions. See text for further explanation.

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) + I_o\alpha = 0; \text{ and,} \quad (16)$$

$$\Sigma F_x = -F_m \cos \theta_1 + F_g \cos \theta_2 - F_1 \cos \theta_3 + F_c + F_h = 0; \text{ and,} \quad (17)$$

$$\Sigma F_y = F_m \sin \theta_1 - F_g \sin \theta_2 - F_1 \sin \theta_3 - F_t - F_v = 0. \quad (18)$$

It is obvious from equation 16 that the torques of the F_g and F_1 forces must be subtracted from the torque of the muscle force for one to determine the torque available to accelerate bone 2 about its center of rotation. The moment of inertia depends on the distribution of the mass of the bone and any other mass that may be attached to the bone. If the force F_1 does not have any associated mass (such as if it were a spring attached to the bone), then it would not contribute to the moment of inertia. But if this force is associated with a mass (such as if this force were the pull of gravity of an object held at point P), then the mass of this object must also be included in the moment of inertia of the system. Note that F_c is increasing steadily with time as the angular velocity of the bone increases while F_t is constant. Because of the presence of the F_c and F_t terms, the

F_h and F_v (and consequently the resultant force F_a) terms differ from those in equations 14 and 15, and generally are smaller.

In a few cases, such as propalinal chewing in mammals, bone 2 moves past bone 1 in a certain direction; this linear movement may occur with or without rotation of bone 2. As with rotational movement, the cases of linear movement without acceleration or deceleration are so rare that they can be ignored. The force required for linear acceleration is provided by the several forces acting on bone 2. Analysis of this acceleration can be done by the decomposition of the acceleration and the forces causing it into rectilinear components. (It may be noted that the analysis of movements of bone 2 which are a combination of rotational and linear movement may be handled more easily with the method of instant centers, such as employed by Frazzetta, 1966.) In the case in which the contraction of the muscle results in linear movement of bone 2 without any rotational movement[1] (propalinal chewing in mammals), the equations are:

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) = 0; \text{ and} \quad (19)$$

$$\Sigma F_x = -F_m \cos\theta_1 + F_g \cos\theta_2 - F_1 \cos\theta_3 + F_h + ma_x = 0; \text{ and} \quad (20)$$

$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 - F_1 \sin\theta_3 - F_v - ma_y = 0, \quad (21)$$

in which m is the mass of bone 2 and a_x is the acceleration along the x-axis and a_y is the acceleration along the y-axis. Again if force F_1 is associated with a mass attached to bone 2, then this mass must be included in the mass undergoing linear acceleration. The equations for bone 2 undergoing both angular and linear equations may be left to the reader.

The various equations, 13–21, describe the consequences resulting from the contraction of a simple one-joint muscle and from the actions of all other forces acting on this bone-lever system. The proper set of equations must be chosen according to the rectilinear and rotary conditions of the system. The number of muscular or other forces acting on the bones does not complicate the equations other than by including additional terms to be added algebraically. A term must be present in the sum of the moments for each torque-producing force, and a term must be present in each sum of the rectilinear component forces for each force. In addition, a term for the inertia torque and the radial and tangential inertia forces must be included, if the bone is undergoing angular acceleration, as well as a term for the linear inertia force, if the bone is undergoing linear acceleration (these inertia forces may be considered as fictitious torques or forces under the notion of d'Alembert's principle). It is important to note that the force vectors F_m and F_a do not constitute a

[1] In such cases, frictional forces would generally exist and must be included in the equations.

force couple acting on bone 2 except by rare chance depending on the magnitudes and directions of the several actual and fictitious forces acting on this bone.

A few additional examples may serve to illustrate the general applicability of free-body diagrams to muscle analysis as well as showing some special points; not all possible conditions are treated. In the following cases, the muscle is a one-joint muscle, and the general conditions are the same as those specified above for figure 5.

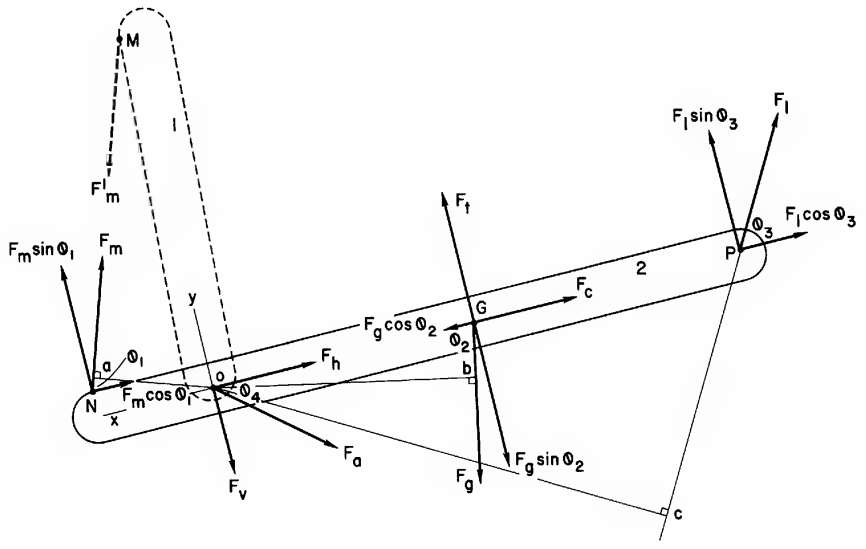

FIG. 6. Schematic drawing of a one-joint extensor muscle and free-body diagram of bone 2. The system is under the same conditions as in figure 5. See text for further explanation.

AN EXTENSOR MUSCLE: The arrangement of forces in a simple one-joint extensor muscle, such as the triceps (part) in man, is shown in figure 6. Under static conditions of bone 2, the equations for the sum of the moments and of the force vectors are:

$$\Sigma M_o = F_m(oa) + F_g(ob) - F_l(oc) = 0; \text{ and} \quad (22)$$
$$\Sigma F_x = F_m \cos\theta_1 - F_g \cos\theta_2 + F_l \cos\theta_3 + F_h = 0; \text{ and} \quad (23)$$
$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 + F_l \sin\theta_3 - F_v = 0. \quad (24)$$

When bone 2 is undergoing angular acceleration, these equations are:

$$\Sigma M_o = F_m(oa) + F_g(ob) - F_l(oc) - I_o\alpha = 0; \text{ and} \quad (25)$$
$$\Sigma F_x = F_m \cos\theta_1 - F_g \cos\theta_2 + F_l \cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (26)$$
$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 + F_l \sin\theta_3 + F_t - F_v = 0. \quad (27)$$

In this case, it should be noted that the pull of gravity assists rather than opposes the muscle force, e.g., gravity adds to the clockwise torque required for angular acceleration of the bone as expressed in equation 25. It should also be noted that, because of the arrangement of the system, the radial inertia force acts in the same direction as the x-component of the muscle force; consequently, the muscle force does not provide any

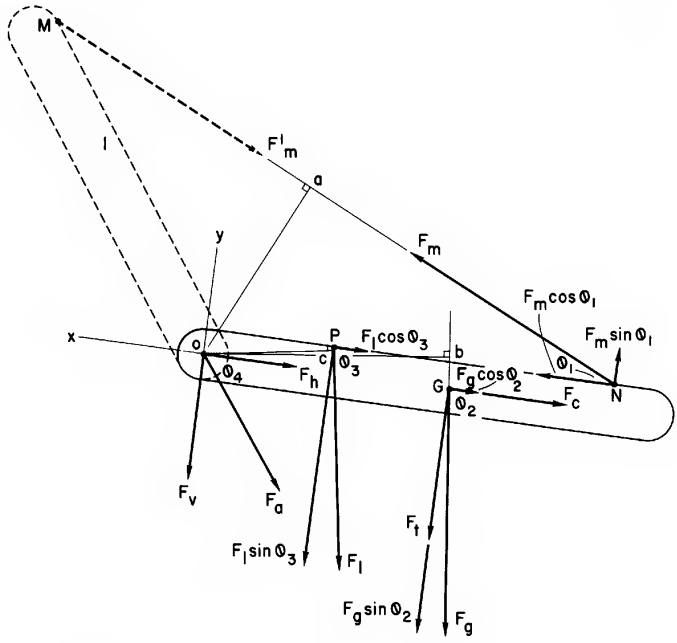

FIG. 7. Schematic drawing of a one-joint flexor muscle and free-body diagram of bone 2. The system is the same as in figure 5 except for the locations of the muscle force and the load force. See text for further explanation.

of the needed centripetal force. Because of the arrangement of forces, I would expect that the x-component of the articular force, F_h, would be directed toward the left, not toward the right as shown in figure 6. The correct direction for this component will be apparent when values are substituted for the other terms and the equation solved for F_h.

A FLEXOR EXAMPLE: The arrangement of forces in a simple one-joint flexor muscle in which the muscle inserts on bone 2 distal to the points at which the other forces act is shown in figure 7, this arrangement being the condition of a second-class lever. This system is seen in some mammalian jaws in which the molar teeth engage an object behind the attachment of the adductor muscles.

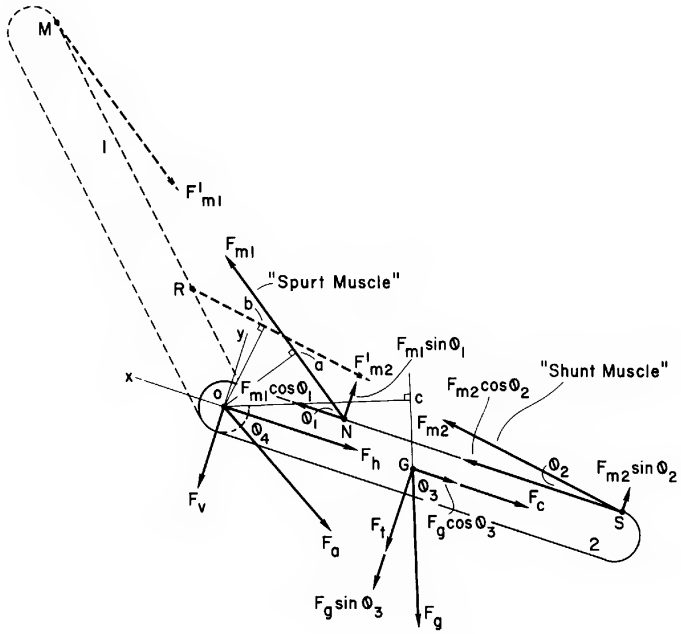

FIG. 8. Schematic drawing of a one-joint "spurt muscle" and a one-joint "shunt muscle" and free-body diagram of bone 2. The system is the same as in figure 5 except that the load force is omitted. See text for further explanation.

Under static conditions, the sums of the moments and of the vector forces are:

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) = 0; \text{ and} \quad (28)$$
$$\Sigma F_x = -F_m \cos\theta_1 + F_g \cos\theta_2 + F_1 \cos\theta_3 + F_h = 0; \text{ and} \quad (29)$$
$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 - F_1 \sin\theta_3 - F_v = 0. \quad (30)$$

Under conditions of angular acceleration, the equations are:

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) + I_o\alpha = 0; \text{ and} \quad (31)$$
$$\Sigma F_x = -F_m \cos\theta_1 + F_g \cos\theta_2 + F_1 \cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (32)$$
$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 - F_1 \sin\theta_3 - F_t - F_v = 0. \quad (33)$$

Note that except for a difference in sign of the $F_1 \cos\theta_3$ term because of a difference in the vector direction of force F_1, equations 28–33 are identical to equations 13–18, although the former equations describe the action of a second-class lever, whereas the latter equations describe the action of a third-class lever. The differences between these cases lie, of course, in the values for the several terms. For the same muscle force under static conditions, the load force F_1 will be greater in the present case (as shown

in equation 28) than in the previous case (as shown in equation 13). Moreover, when the muscular and other forces are arranged as shown in figure 7, a tensile force generally exists at the articulation along the y-axis tending to pull the bones apart instead of the compression force seen in the previous cases. The collagenous fibers of the articular capsule and associated ligaments would resist this tensile force.

"SPURT" AND "SHUNT" MUSCLES: Recently, Basmajian (1959, 1962, pp. 63–67; see also Hall, 1965, pp. 33–34) discussed the mechanics of the biceps, brachialis, and the brachioradialis which are all flexors of the elbow joint. He described the brachioradialis as a "shunt" muscle that acts during rapid flexion and provides centripetal force along the long axis of the moving bone. The biceps and the brachialis are "spurt" muscles that provide the force for angular acceleration. With the help of electromyography, Basmajian provided apparent experimental support for the earlier theories of MacConaill (1946, 1949). Unfortunately, Basmajian's analysis of "spurt" and "shunt" muscles does not include a consideration of all the forces, muscle and other, acting on the bone-lever system. Moreover, MacConaill's mechanical treatment is incomplete and vague on some important points, so that a complete re-analysis of the mechanical properties of "shunt" and "spurt" muscles[1] is desirable.

The arrangement of the biceps and the brachialis (the "spurt" muscles) and of the brachioradialis (the "shunt" muscle) are shown schematically in figure 8, with the use of the same conventions as in figure 5. The biceps has been shown as a one-joint muscle for this purpose which does not affect the general conclusions. No load has been placed at the distal end of bone 2, as this would only add another term to all the equations without increasing the clarity or the general application of the analysis. Bone 1 is fixed, and bone 2 is free to rotate. The vectors of the two muscle forces are placed so that their moment arms are equal in length. The magnitudes of the forces F_{m1} and F_{m2} have been set equal, so that the various consequences of these forces can be compared readily. I consider only the condition of angular acceleration, which is the only one pertinent to the

[1] It is not easy to determine from Basmajian's and MacConaill's papers exactly what was meant by "spurt" muscles, whether these muscles provide a large torque for angular acceleration or a large force in the tangential direction (which may or may not produce a large torque) or both. MacConaill stated that "spurt" muscles provide a force along the tangent to the curve of movement of the bone (which is not the same as the tangential inertia force) but also wrote that this force rotates the bone (i.e., provides the angular acceleration). These two properties are not the same, and one does not imply the other. A muscle could provide a large force in the tangential direction and little torque, and vice versa. Because these workers stated that spurt muscles displace the bone along a curve (rotate it), I assume that they mean that "spurt" muscles provide large torques, although I realize that neither author stated so clearly.

consideration of "spurt" and "shunt" muscles.

If each muscle is considered separately, then the sums of the moments and of the vector forces for the "spurt" muscle are:

$$\Sigma M_o = -F_{m1}(oa) + F_g(oc) + I_o\alpha = 0; \text{ and} \quad (34)$$
$$\Sigma F_x = -F_{m1}\cos\theta_1 + F_g\cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (35)$$
$$\Sigma F_y = F_{m1}\sin\theta_1 - F_g\sin\theta_3 - F_t - F_v = 0. \quad (36)$$

For the "shunt" muscle, these equations are:

$$\Sigma M_o = -F_{m2}(ob) + F_g(oc) + I_o\alpha = 0; \text{ and} \quad (37)$$
$$\Sigma F_x = -F_{m2}\cos\theta_2 + F_g\cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (38)$$
$$\Sigma F_y = F_{m2}\sin\theta_2 - F_g\sin\theta_3 - F_t - F_v = 0. \quad (39)$$

When the "spurt" and the "shunt" muscles act together, these equations are:

$$\Sigma M_o = -F_{m1}(oa) - F_{m2}(ob) + F_g(oc) + I_o\alpha = 0; \text{ and} \quad (40)$$
$$\Sigma F_x = -F_{m1}\cos\theta_1 - F_{m2}\cos\theta_2 + F_g\cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (41)$$
$$\Sigma F_y = F_{m1}\sin\theta_1 + F_{m2}\sin\theta_2 - F_g\sin\theta_3 - F_t - F_v = 0. \quad (42)$$

Comparing the effects of the forces developed by the "spurt" muscles and the "shunt" muscles, we see that the torque produced by each muscle is the same, because the force and the moment arm of each muscle were set equal. Thus each muscle could impart the same amount of angular acceleration to bone 2. If the duration of the acceleration was the same for each muscle, then the angular velocity of bone 2 would be the same as would be the needed centripetal and tangential forces on bone 2. But the component forces along the x-y axes differ for each muscle. Force F_{m1} intersects the x-axis at a greater angle than does force F_{m2}; consequently, the force $F_{m2}\cos\theta_2$ is greater than force $F_{m1}\cos\theta_1$ (along the x-axis), whereas force $F_{m1}\sin\theta_1$ is greater than force $F_{m2}\sin\theta_2$ (along the y-axis). The component force acting along the x-axis would provide the radial acceleration and the component of force acting along the y-axis would provide the tangential acceleration needed to keep bone 2 moving in a circular path about its articulation. There is no question that the "shunt" muscle, which intersects the x-axis at a small angle, *could* provide a larger force for radial acceleration as has been advocated by MacConaill and Basmajian. I must emphasize that the "shunt" muscle *could* provide a greater centripetal force if *needed,* but neither MacConaill nor Basmajian nor I have shown yet that this greater amount of centripetal force is needed. It is tempting to conclude, as MacConaill and Basmajian implied (see footnote, p. 20), that the "spurt" muscle would provide more force for tangential acceleration, but it should be obvious that the "spurt" and the "shunt" muscles in the present case impart the same amount of

tangential acceleration onto bone 2 because they impart the same amount of angular acceleration onto this bone. Hence, apparently, several important points were left unanswered in these earlier studies.

The magnitude of the components of each muscle force in the directions of the centripetal and tangential forces had not been determined and compared to the *required* centripetal and tangential forces. If a muscle, either the "spurt" or the "shunt" muscle in this example, contracts, it develops a certain amount of force along a certain vector direction. This force produces a moment, depending on the length of its moment arm, and this moment will impart a certain angular acceleration onto the bone, depending on its moment of inertia. Because of its angle of insertion with the bone, the muscle force will have a rectilinear component of force along the longitudinal axis of the bone and a component of force at right angles to this axis. For each force produced by the muscle, the magnitudes of the torque and of each component force are fixed because of the arrangement of the bones and the muscle. The consequences of each component force are here discussed separately.

The component of the muscular force along the longitudinal axis of bone 2 provides part of or all the centripetal force required to keep this bone moving in a circular direction. The amount of centripetal force required depends on the angular velocity of the bone, hence it will vary as the bone rotates. Only rarely will the force component of the muscle along the x-axis be exactly equal to the amount of centripetal force needed to keep the bone rotating about the articulation. When more force is available than needed as centripetal force, the excess force pushes bone 2 against bone 1; this appears as the F_h term in the equations. When less force is produced by the muscle along the x-axis than the needed centripetal force, the bone tends to move away from the center of rotation. The additional centripetal force required to keep the bone rotating about the articulation is provided by the resistance of the collagenous-fibered articular capsule and the ligaments about the articulation.

No empirical measurements have ever been taken of the "centripetal force component" of "shunt" and "spurt" muscles compared with the levels of centripetal force required. Certainly a "shunt" muscle produces a larger "centripetal force component" than does a "spurt" muscle, but it is possible that the "centripetal force component" of each muscle is more than sufficient to keep the bone rotating about the articulation. If so, then the only difference would be that the "shunt" muscle would push bone 2 against bone 1 with greater force than would the "spurt" muscle. Or it is possible that the ligaments of the articulation are more than strong enough to provide the needed centripetal force by resisting

the centrifugal pull of bone 2. Hence the "centripetal force component" of the muscle may not be essential, although it is present. Moreover, in some muscles, such as the extensor muscle shown in figure 6, the direction of the force vector is such that none of the centripetal force is provided by the muscle. Indeed the component of the muscle along the x-axis will oppose the centripetal force. In this case most of the centripetal force is provided by the resistance of the collagenous fibers at the articulation.

Consideration of the tangential force differs somewhat from the discussion of centripetal force, because the amount of angular acceleration depends directly on the amount of tangential acceleration which in turn depends on the "tangential force component" of the muscular force and the moment arm of this force vector. Hence the "spurt" muscle has a larger force component in the direction of the tangential acceleration and a smaller moment arm, whereas the "shunt" muscle has a smaller force component and a larger moment arm. The torque produced by each force component in the direction of the tangential acceleration is the same; thus the "shunt" muscle and the "spurt" muscle in this example impart the same angular acceleration to bone 2. These muscles differ, however, in the amount they pull bone 2 against bone 1 along the direction of the y-axis. Because the "spurt" muscle has a larger component of force along the y-axis than does the "shunt" muscle, it will pull bone 2 against bone 1 more forcefully; this will show up as a larger F_v term in the case of the "spurt" muscle.

With increased angular acceleration on a bone, more moment-producing force is needed. Both "spurt" and "shunt" muscles contribute force to the torque needed for angular acceleration (one could also say "force for tangential acceleration"). It should be emphasized that only the force and the moment arm are essential to the magnitude of the torque; no other factors are needed, but these two are essential. A "shunt" muscle could have a larger torque than a "spurt" muscle of equal force only if its moment arm is longer. MacConaill's notion that "spurt" muscles (i.e., those that impart more angular acceleration to a bone) direct more of their force across the bone than along it (1949, p. 100) is not meaningful. A muscle could direct most of its force across a bone but have an extremely short moment arm and hence develop little torque. Other muscles could pull along a bone but have a large moment arm and thus produce a large torque. "Spurt" muscles do provide a large component of force in the direction of the tangential acceleration, but this force by itself is not sufficient to rotate a bone.

If all moment-producing forces contribute to the torque needed for angular acceleration, then Basmajian's (1959) electromyographic obser-

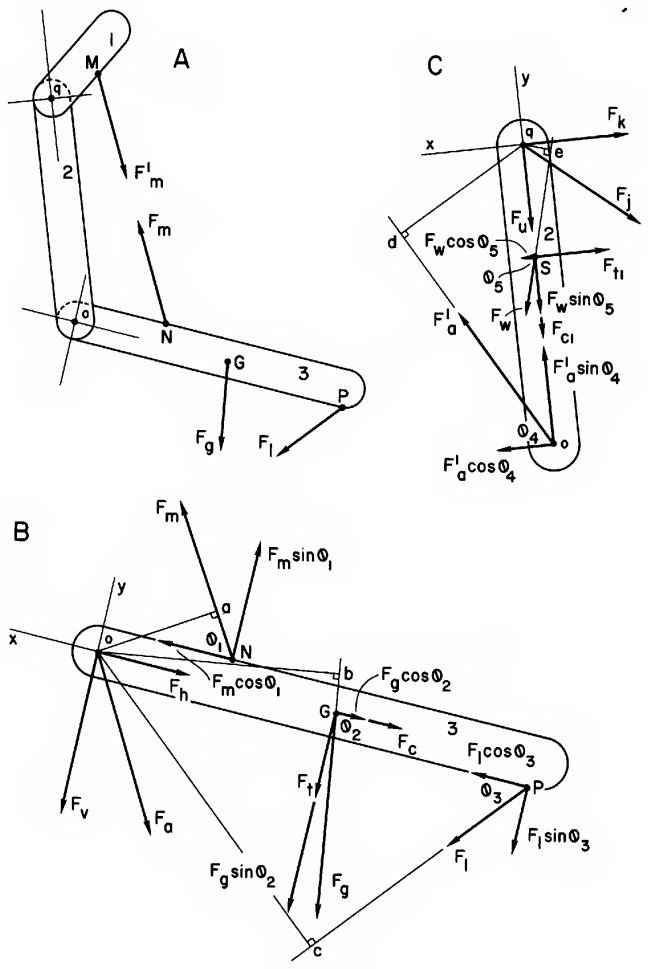

FIG. 9. Schematic drawing and free-body diagram of a two-joint muscle. A. Two-joint flexor muscle. B. Free-body diagram of bone 3. C. Free-body diagram of bone 2. See text for further explanation.

vations may allow several interpretations. His observations were, briefly, that during slow flexion of the elbow, the "spurt" muscles were active while the "shunt" muscles were relatively quiescent, but in quick flexion the "shunt" muscles were active as were the "spurt" muscles. Basmajian concluded that the "shunt" muscles were active during fast flexion to provide the larger centripetal force needed in fast flexion. Although it is absolutely true that considerably more centripetal force is needed during rapid flexion, and although the "shunt" muscle would produce a large

centripetal force, there is no reason on the basis of Basmajian's observations to conclude that the primary reason for the contraction of the "shunt" muscle (the brachioradialis) during rapid flexion was to provide the needed centripetal force. No evidence was presented showing that the ligaments of the articulation could not provide the necessary centripetal force during rapid flexion, or that the "spurt" muscles were not providing sufficient centripetal force. Another explanation is available to explain Basmajian's experimental observations. In slow flexion of the elbow joint, less torque and hence less muscular force are required. During rapid flexion, more torque and hence more force are needed to produce the greater angular acceleration on the bone. Hence, I suggest that the activity of the "shunt" muscles during rapid flexion is primarily to provide sufficient torque for the greater angular acceleration. No doubt can exist that increased angular acceleration requires increased muscular force, whereas increased centripetal force can be provided by the resistance of articular ligaments.

Basmajian (1962, fig. 43) has also published the electromyograms of the flexor muscles during quick flexion of the elbow joint with and without a load. The "shunt" muscle is less active than the other flexors without a load, and all the muscles are almost equally active with a load. But the activity of the "spurt" muscles also appears to be greater with a load than without a load. Although no data are available for testing the several explanations for the observed facts, I believe that the need for increased moment-producing force is very important. I do not gainsay the fact that the "shunt" muscles provide a considerable "centripetal force component" in addition to increased torque, but I do not believe that the increased "centripetal force component" provided by "shunt" muscles is the primary reason for their evolutionary development or for their contraction during rapid flexion.

A reasonable explanation for the varied arrangement of muscles, such as the several flexors of the elbow joint, is that selection would favor an arrangement that has the optimum distribution of forces.[1] Certainly an

[1] After the manuscript was completed, I received a copy of Friedrich Pauwels' "Gesammelte Abhandlungen zur funktionellen Anatomie des Bewegungsapparates" (1965), which provides a possible explanation for the arrangement of muscle sets such as the several flexors of the elbow joint. With the help of photoelastic techniques, Pauwels showed (pp. 226–231) that the stress within the long bones of the arm is less when both sets of flexor muscles ("spurt" and "shunt") contract than when only one set is active. Hence the explanation for the distribution of elbow flexors may be to reduce the maximum stress within the bones of the forearm—an explanation that is quite outside the realm of free-body diagrams as used in this study, and quite outside any notion of reducing the centripetal force on the rotating bone.

arrangement in which the muscles provide both the needed centripetal and tangential accelerations is more advantageous than an arrangement of muscles that provides only one of these accelerations. Probably the elbow flexors evolved for reasons such as these. However, activity in a muscle of this group during any flexion is probably governed by the amount of moment-producing force needed for angular acceleration.

The notion of "spurt" and "shunt" muscles should be dropped in favor of free-body diagrams, because these terms refer to only one of the several functions of muscles in the bone-muscle system and because they strongly tend to deny the existence of the other functions of muscles.

TWO-JOINT MUSCLES

The two-joint muscle can be analyzed exactly as the one-joint muscle except that a free-body diagram must be drawn for each bone. Because three bones are involved, a larger number of movements are possible. In all cases, I consider the bone from which the two-joint muscle takes origin to be fixed in position, whereas the other bones are movable. The following analyses of two-joint muscles are based on the same general assumptions used for the one-joint muscle, but the series of examples are simpler. No reason exists, for example, for repeating the analysis in a gravity-free condition or for treating linear acceleration. The relationship between the direction of the force vector of the muscle and the longitudinal axis of the central bone of the three-bone series is of special interest and is emphasized.

A simple two-joint flexor muscle, such as the biceps in man, is shown in figure 9A, with the muscle originating from bone 1 at point M and inserting on bone 3 at point N; the mass of the muscle is ignored. When this muscle contracts, it exerts an equal and opposite tensile force, F_m and F'_m, on bones 1 and 3; the consequences of this force depend on all the other forces acting on the bones and the arrangement of the bones. Bones 2 and 3 are free to rotate only. Note that the orientation of the x-axis and the y-axis differs for bones 2 and 3; in each case one of the axes lies along the longitudinal axis of the bone.

In the first case, bone 3 is assumed to be *initially* under static conditions relative to bone 2, with moment-producing forces F_m, F_g, and F_1 acting on it as shown in figure 9; the free-body diagram for bone 3 is shown in figure 9B. Thus, the equations for the sum of the moments and for the vector forces for bone 3 are:

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) = 0; \text{ and} \quad (43)$$

$$\Sigma F_x = -F_m \cos\theta_1 + F_g \cos\theta_2 - F_1 \cos\theta_3 + F_h = 0; \text{ and} \quad (44)$$

$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 - F_1 \sin\theta_3 - F_v = 0. \quad (45)$$

The magnitudes and directions of the forces F_h and F_v depend, of course, on the algebraic sum of the other forces acting along the x-axis and the y-axis. If these forces are as shown in figure 9B, then F_a is the resultant force and is the force exerted by bone 2 on bone 3 at their articulation. (Force F_a can also be found by direct vector summation of the forces acting on bone 3.) It should be noted that, except for very special cases, a force F_a will exist at the articulation of bone 3 under the action of a two-joint muscle.

If a force F_a acts on bone 3 at its articulation with bone 2, then the equal and opposite reaction force, F'_a, will act on bone 2 at its articulation; force F'_a is the force exerted by bone 3 on bone 2 under the action of the two-joint muscle. The consequences of this force on bone 2 must be analyzed relative to the center of rotation, q, of bone 2, which is situated at the articulation of bone 2 with bone 1. Bone 2 is free to rotate only; the free-body diagram for bone 2 is shown in figure 9C. Thus, the equations for the sum of the moments and for the vector forces for bone 2 are:

$$\Sigma M_q = F'_a(qd) + F_w(qe) - I_q\alpha_1 = 0; \text{ and} \quad (46)$$

$$\Sigma F_x = -F'_a \cos\theta_4 - F_w \cos\theta_5 + F_{t1} + F_k = 0; \text{ and} \quad (47)$$

$$\Sigma F_y = F'_a \sin\theta_4 - F_w \sin\theta_5 - F_{c1} - F_u = 0. \quad (48)$$

in which F_w is the force of gravity on bone 2, F_k and F_u are the components of the force, F_j, acting on bone 2 at the articulation, and F_{c1} is the centripetal, and F_{t1} is the tangential inertia force of bone 2 when it is undergoing radial acceleration (α_1). Thus bone 2 is undergoing clockwise angular acceleration. Another force, muscular or other, would have to act on bone 2 in a counterclockwise direction to maintain this bone in a static state.[1] This force could be a one-joint flexor muscle running from bone 1 to bone 2 (not shown in fig. 9 to preserve clarity). In this case the equations for static equilibrium would have to be written for bone 2. With the contribution of this one-joint muscle, bones 1 and 2 would be equivalent to a single rigid body, and the two-joint muscle would act as a one-joint muscle.

The result of all torque-producing forces acting on bone 3, which is initially in a static condition relative to bone 2, is a force, F'_a, acting on bone 2 at point o, except for the rare case in which the vector sum of these

[1] In the rare case in which $F'_a(qd)$ is equal and opposite to $F_w(qe)$, bone 2 does not rotate about bone 1; no $I_q\alpha_1$ term exists in equation 46, no F_{t1} term in equation 47, and no F_{c1} term exists in equation 48. This is one case in which the action of a two-joint muscle by itself would result in static equilibrium of both bones 2 and 3. The other possible case may be one in which the forces on bone 3 balance each other so that no F_a force exists at the articulation, and in which the vector of the F'_a force on bone 2 passes through the center of rotation (point q) of this bone.

torque-producing forces is equal to zero. Force F'_a produces a torque on bone 2 which rotates about point q. When bone 2 begins to rotate about point q, the relationships of forces F_m, F_g, and F_1 to bone 3 are altered so that the sum of their torques relative to point o will, except by rare chance, no longer be equal to zero. Hence bone 3 will start to rotate about its center of rotation. Thus, except for a few rare arrangements of forces, the contraction of a single two-joint muscle cannot by itself maintain the bone-lever system in a condition of static equilibrium—a two-joint muscle-bone system is an inherently non-static system. Even the few rare cases mentioned are ones of unstable equilibrium. At least, one additional torque-producing force must act on bone 2 to guarantee static equilibrium. A one-joint muscle between bones 1 and 2 would be most advantageous, because it could develop a varying amount of force to balance the other torque-producing forces acting on bone 2. Only when the central bone (2) is maintained in static equilibrium can the distal bone (3) retain its initial static equilibrium with the contraction of a two-joint muscle.

If, under the action of the two-joint muscle, bone 3 is undergoing angular acceleration, then the equations for the sums of the moments and for the vector forces are:

$$\Sigma M_o = -F_m(oa) + F_g(ob) + F_1(oc) + I_o\alpha = 0; \text{ and} \quad (49)$$

$$\Sigma F_x = -F_m \cos\theta_1 + F_g \cos\theta_2 - F_1 \cos\theta_3 + F_c + F_h = 0; \text{ and} \quad (50)$$

$$\Sigma F_y = F_m \sin\theta_1 - F_g \sin\theta_2 - F_1 \sin\theta_3 - F_t - F_v = 0, \quad (51)$$

in which F_c is the centripetal inertia force and F_t is the tangential inertia force of bone 3. Again, the magnitudes and directions of forces F_h and F_v depend on the algebraic sum of all other force components along the x-axis and the y-axis. If these forces are as shown in figure 9, then F_a is the resultant force and is the force exerted by bone 2 on bone 3; the equal and opposite reaction force, F'_a, acts on bone 2 and can be analyzed as discussed above. Again, as shown above, bone 2 will usually rotate relative to bone 1 unless an additional torque-producing force, e.g., the contraction of a one-joint muscle, is present.

It is apparent from these analyses that, except in rare cases, the center of rotation of bone 3 in a two-joint muscle-bone system is never stationary but moves as bone 2 rotates. Thus the relationships of the forces to bone 3 are constantly changing and could not be analyzed easily with the above equations. These forces might be analyzed with an approach using instant centers but even this would be difficult. It must be stressed that the analysis of the movement of the central bone depends on one's knowing force F_a, which can be determined only after analyzing all the forces on the distal bone, which depends on the position and hence the move-

ment of the central bone. At this point, theoretical treatment becomes most difficult indeed, and the best approach is a series of empirical observations.

One of the pertinent problems associated with two-joint muscles is the relationship between (a) the direction of force vector F_m of the muscle and the longitudinal axis of the central bone, i.e., where these two lines intersect, and (b) the direction of the resultant force by the distal bone upon the central bone—the vector direction of the F'_a force. It is very tempting to conclude that, if F_m is parallel to the axis o–o_1 (fig. 10A), the central bone undergoes pure compression and does not rotate; if F_m intersects axis o–o_1 below point o (fig. 10B), the central bone rotates counterclockwise; and, if F_m intersects axis o–o_1 above point o_1 (fig. 10C), bone 2 rotates clockwise. This conclusion follows from the notion that a muscle contraction places a force couple on the bone (e.g., Gray, 1944, 1956) and has been applied in a general way to two-joint muscles by Fischer (1906, p. 51), R. Fick (1910, pp. 33–337), and Manter (1938, pp. 535–536), and, in a special case, by Zusi (1959).[1] However, force couples never occur except by rare chance, as is discussed above for the one-joint muscle (see p. 16, and below, p. 33). Either the pull of gravity or some other force acts on distal bone 3 in addition to the pull of the muscle, or bone 3 will undergo angular acceleration, in which case a centripetal and a tangential inertia force will exist. Thus, no direct relationship exists between the direction of the vector of the muscular force F_m and the movement of the central bone. An exact relationship does not even exist between the direction of force vector F'_a (the force exerted by bone 3 on bone 2 at their articulation) and the movement of bone 2 because of the effect of gravity on the central bone. However, the following relationships generally hold for the muscle-bone system shown in figure 10. If F'_a lies along the y-axis, then bone 2 suffers compression or tension, but it does not rotate. If F'_a lies in one of the two negative x-quadrants (to the left), then bone 2 will rotate clockwise, and, if F'_a lies in one of the two positive x-quadrants, then bone 2 will rotate counterclockwise. But the direction of force vector F'_a may be obtained only after all the necessary terms in the equations are solved for the F_h and F_v forces. The resultant force, F'_a, will vary for the same muscle force F_m, depending on the magnitude and

[1] Unfortunately my earlier correction (Bock, 1964, pp. 16–17) of Zusi's discussion is in error. Both Zusi and I had failed to include all the forces acting on the mandible and quadrate in our analysis. The source of these errors should be apparent from the general conclusions of the present paper. The mechanics of the morphological system described by Zusi can be analyzed with the help of free-body diagrams.

direction of the other forces acting on bone 3, on whether bone 3 is under static conditions or being accelerated, and on the mass and the moment of inertia of bone 3. Thus it is not possible to determine, by inspection alone of the morphological diagram of the forces resulting from the contraction of a two-joint muscle, what consequence it will have on the central bone of the system. The free-body diagrams for both the distal

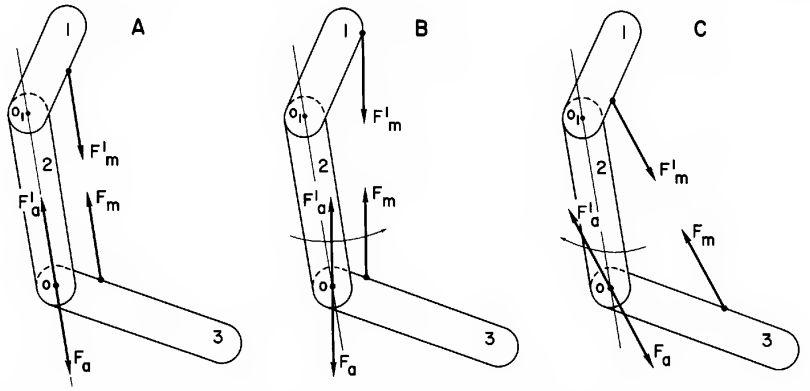

FIG. 10. Schematic drawings of a two-joint muscle to show the (presumed) relationship between the vector of the muscle forces, the longitudinal axis of bone 2, and the rotation of bone 2. A. The vector of the muscle force and axis o–o_1 are parallel. B. These lines intersect below point o. C. These lines intersect above point o_1. The thin curved arrow shows the movement of bone 2. The analysis illustrated in this figure is incomplete and incorrect and should not be followed. See text for further explanation.

and central bones must be completed before the movement of the central bone is known. This limitation is not a weakness of the method of free-body diagrams but a consequence of the fact that certain calculations must be made before the diagrams can be completed. This limitation does mean that in any study of two-joint muscles a complete analysis cannot be based only on study of the morphological form of the bone-muscle system. No matter how carefully the muscles and bones are dissected and described, the effect of the muscle on the central bone of the system (and hence on the distal bone) cannot be determined by a simple examination of the morphology of the bone-muscle relationships.

GENERAL THREE-DIMENSIONAL MODEL

In the above analysis of one-joint and two-joint muscles, I have assumed that the pull of the muscle lies in the plane containing the moving

bone and the stationary bone. In most cases, this assumption is either realized, or the deviation of the muscle pull from this plane is so small that it can be ignored. However, in some cases, as in certain avian and mammalian jaw muscles, the pull of the muscle is well off the plane containing the bones. An abbreviated model is presented to illustrate the general method for treating muscles in which the tensile force is not in

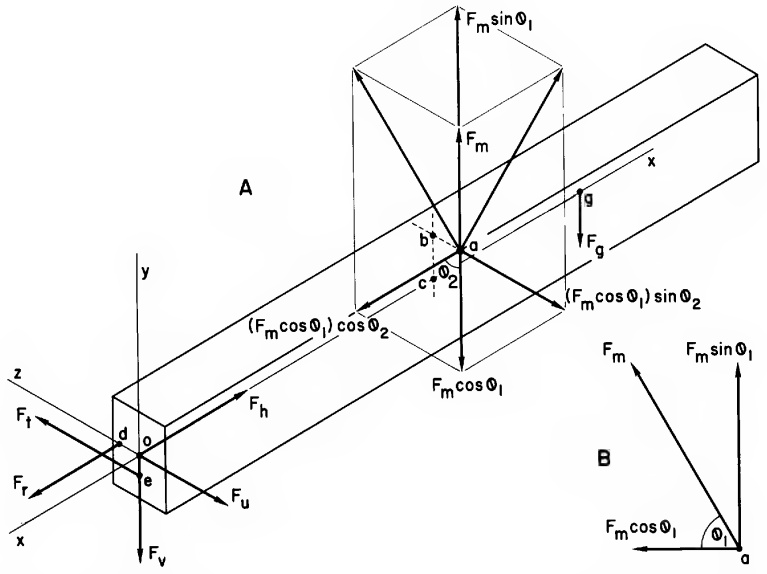

FIG. 11. A. Free-body diagram of a one-joint muscle, the pull of which is not coplanar with the plane of rotation of the bone. B. The decomposition of the muscle force F_m. See text for further explanation.

the plane containing the bones. I analyze only a one-joint muscle under static conditions.

Consider a one-joint muscle inserting at point a (fig. 11A; only one bone is shown for clarity). The muscle inserts at an acute angle to each of the three rectilinear axes, x, y, and z, which are oriented with the x-axis along the longitudinal axis of the bone, the y-axis in the plane of rotation of the bone, and the z-axis coinciding with the axis of rotation of the bone. Torques relative to the point center, o, may exist in all three planes; however, the bone can rotate only in the x-y plane about the z-axis. The insertion of the muscle, point a, does not lie on any of the three axes. Point b lies in the x-y plane and is the same distance from the x-z and the y-z planes as is point a. Point c lies on the x-axis in the x-y

plane and is the same distance from the y-z plane as is point a. Force vector F_m of the muscle is superimposed on the vector $F_m \sin \theta_1$ in figure 11A.

The force F_m must first be decomposed into its three component forces along the x, y, and z axes. A plane, perpendicular to the x-z plane, is passed through the vector F_m (fig. 11B). Vector F_m can be decomposed into two components, one parallel to the y-axis, $F_m \sin \theta_1$, and one lying in the x-z plane, $F_m \cos \theta_1$. The vector $F_m \cos \theta_1$ can be decomposed further into two components, one parallel to the x-axis, $(F_m \cos \theta_1) \cos \theta_2$, and one parallel to the z-axis, $(F_m \cos \theta_1) \sin \theta_2$. Each of these components is a moment-producing force on the bone; they act in pairs in each plane. They can be treated in the normal way with the use of free-body diagrams with three torque and three linear force equations.

The equations for the sum of the moments are (for static conditions):

$$\Sigma M_{x-y} = -F_m \sin \theta_1(oc) - (F_m \cos \theta_1) \cos \theta_2(cb) + F_g(og) = 0; \text{ and} \quad (52)$$

$$\Sigma M_{x-z} = (F_m \cos \theta_1) \sin \theta_2(oc) + (F_m \cos \theta_1) \cos \theta_2(ab) - F_r(od) = 0; \text{ and} \quad (53)$$

$$\Sigma M_{y-z} = (F_m \cos \theta_1) \sin \theta_2(bc) - F_m \sin \theta_1(ab) + F_t(oe) = 0. \quad (54)$$

Force F_g is the force of gravity at the center of gravity g. The forces F_r and F_t are the resistances of bone, ligaments, and other tissues of the articulation against torques in the x-z and the y-z planes; these forces are concentrated at points d and e.

The equations for the sums of the vector forces are (for static conditions):

$$\Sigma F_x = -(F_m \cos \theta_1) \cos \theta_2 - F_r + F_h = 0; \text{ and} \quad (55)$$

$$\Sigma F_y = F_m \sin \theta_1 - F_g - F_v = 0; \text{ and} \quad (56)$$

$$\Sigma F_z = (F_m \cos \theta_1) \sin \theta_2 - F_t + F_u = 0. \quad (57)$$

These equations can be expanded if additional forces act on the bone, or if the bone rotates, or if the bone moves in some linear direction. The expansion of the equation would follow the same form as shown above except that the forces and movements must be considered in three dimensions instead of two, which may make the equations messier in appearance, but no more complicated.

Two-joint muscles can be analyzed in the same way, with the only possible problem being increased messiness of the diagrams and of the equations.

DISCUSSION

The analyses of the biomechanical properties of one-joint and two-joint muscles provide the basis for a general consideration of three problems. These are: (a) whether the tensile force of a muscle produces a

simple force couple on the bone to which it inserts; (b) the advantages and disadvantages of two-joint muscles; and (c) the usefulness of free-body diagrams for our understanding of the consequences of a muscle acting in a bone-muscle system. These problems are not independent, because most workers who have discussed two-joint muscles have based

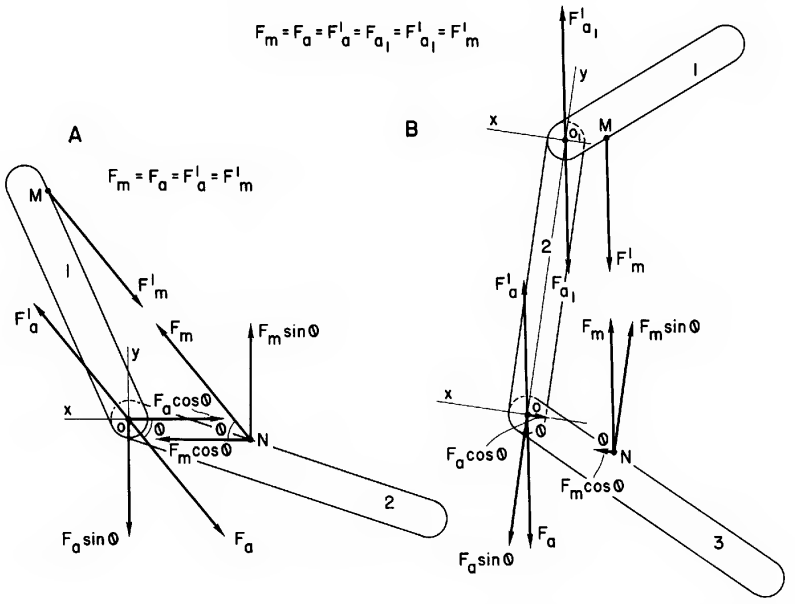

FIG. 12. Schematic drawing to show how the concept of force couples may have developed. A. One-joint flexor muscle. B. Two-joint flexor muscle. In the one-joint muscle, forces F_m and F_a constitute a force couple on bone 2, whereas forces F'_m and F'_a constitute a force couple on bone 1. In the two-joint muscle, forces F_m and F_a constitute a force couple on bone 3, and so forth. The analysis illustrated in this figure is incomplete and incorrect and should not be followed. See text for further explanation.

part of their analysis on the notion that a muscle produces a force couple on the bone to which it attaches, and because many parts of the discussion depend on the general applicability of free-body diagrams.

MUSCLE ACTION AS A FORCE COUPLE: One of the oldest prevailing ideas in studies on bone-muscle biomechanics is the notion that the tensile force produced by a muscle results in a simple force couple on each of the bones to which the muscle attaches (fig. 12; and see the footnote on page 13). This notion may be traced back as far as A. E. Fick (1856, cited by R. Fick, 1910, p. 328) and doubtless has even older roots. It was firmly

established by 1900 and has been used extensively since then (Bois-Raymond, 1903, pp. 212, 236; Fischer, 1906, pp. 48–52 and elsewhere; R. Fick, 1910, pp. 328–337; Manter, 1938, pp. 534–538; Elftman, 1939a, pp. 341–343; Barclay, 1946, pp. 190–192; and Gray, 1944, p. 99, 1956, p. 203, and 1962, p. 1). Some of these authors used the term "turning couple" without a clear definiton of the term and how it differs from a force couple. However, in all cases, the discussion and figures leave no doubt that these authors used the term "turning couple" as a synonym for "force couple," as used in this paper. This idea has doubtlessly developed from an analysis of only the force exerted by the muscle on the bones of the bone-muscle system. Indeed, if the forces of the muscle and at the articulation shown in figure 12A were decomposed into rectilinear components and added algebraically, their sum would be equal to zero, hence the forces would be balanced (or so the argument would run). In most of these papers (e.g., Manter, 1938, p. 536), the concept that a muscle produces a force couple on each bone to which it attaches is applied in a similar fashion to two-joint muscles (fig. 12B).

Unfortunately, none of the papers examined included a clear statement of how the directions and magnitudes of the resultant force vector at the articulation were determined. Either an earlier work was cited, or the author based his conclusion on an analysis of only the muscle force, as indicated above. (The muscle force was first decomposed into rectilinear components, to which were added opposing force components at the articulation until the vector sums of these forces were equal to zero. The resulting force at the articulation is, then, parallel to, opposite in direction to, and equal in magnitude to, the muscle force—hence the muscle force and articular force constitute a force couple.) Moreover, these papers generally omitted mention of the center of rotation of the bone—whether at the articulation, at the center of gravity, or at some other point. In most cases, the center of rotation would be at the articulation; thus the articular force would pass through the center of rotation and would not produce a moment on the bone. A pair of equal, parallel, but opposite-in-direction forces, of which one passes through the center of rotation, is a trivial type of force couple and one that may best be excluded from treatment of couples in biomechanical studies. However, it should be stressed that, if such a pair of forces having these properties existed, they could be called a couple and analyzed as such.

The difficulties in these earlier treatments lay, I believe, first, in the attempt to analyze the force produced by a muscle in its bone-lever system independently of all other forces in the system, and, second, in the failure of the authors to realize that, whenever a free-body is acted on

by a moment-producing force, a minimum of two forces must act on the free-body aside from any resultant force at the center of rotation.[1] The second force is either a moment-producing force that opposes the moment of the muscle force to maintain the body in static equilibrium, or an inertia torque or inertia force (this could be considered as a fictitious torque or a set of fictitious centrifugal and tangential forces) associated with the angular acceleration of the free-body. No other conditions exist. The size and direction of the resultant force at the articulation (center of rotation) will depend on all the other forces on the body, not only on the muscle force. It should be obvious that the vector addition of the second force or inertia force (most easily done by the algebraic addition of the rectilinear components) to the force of the muscle will result in a force at the articulation that is not equal to, parallel to, and opposite in sense to the vector of the muscle force. It is possible by rare chance that the forces on a bone will be so arranged that the muscular force and the articular force will constitute a force couple. But such is only a rare chance phenomenon that does not violate the general conclusion that the contraction of a muscle does not produce a force couple on each bone onto which the muscle attaches.

This conclusion is in direct variance with the conclusion used for more than a century in biomechanical studies of bone-muscle systems, and for that reason it must be checked carefully and thoroughly. The importance of checking this conclusion lies in the fact that much of the previous literature on bone-muscle biomechanics is based on the notion that muscle contraction places force couples on the bones onto which it attaches; hence the general results of these earlier works must be re-evaluated carefully for their validity to be ascertained. The effect of reversing this basic tenet will probably be less serious than it appears at first glance, because the statement that muscle action produces force couples appears to be cited more frequently than actually used. For example, although Gray (1944, 1956) made the very strong statement that muscle action produces force couples, he overlooked this statement in his correct analysis of the resultant force at the articulation produced by two moment-producing forces which hold a bone in static equilibrium (Gray, 1944, fig. 30a). Manter (1938), in his excellent study, apparently made little or no use of his statement that a muscle produces a force couple on each bone to which it attaches. Perhaps the most serious effect of the earlier conclusion

[1] The last statement may or may not be true for all free bodies; however, it is true for rigid flat bodies that rotate about a fixed axis which constitute all the structures (i.e., bones) that are considered in this study.

that muscle action produces force couples has been in the analysis of two-joint muscles; this is discussed below.

TWO-JOINT MUSCLES: Interest in two-joint muscles dates back to a very early period in functional morphological studies. Much of the literature covered the advantages and, to a lesser extent, the disadvantages of two-joint muscles as compared to one-joint muscles. Much of this earlier discussion is subject to question, because it was based on the notion that muscle action produces force couples. In the case of a two-joint muscle, each of three bones in series was thought to be acted on by a force couple (Manter, 1938, p. 536; and see fig. 12B). Rejection of this conclusion and the application of free-body diagrams to two-joint muscles permit the clarification of the following points.

1. Not all the consequences of a two-joint muscle can be determined from the examination of the relative positions of the three bones and the direction of the force vector. No direct relationship exists between the inclination of the force vector of the muscle to the longitudinal axis of the central bone and the rotation of this bone (see above, p. 29). Separate free-body diagrams must be constructed for the distal and central bones of the system. (I have assumed that in all cases the bone from which the two-joint muscle originates is the "stationary" bone; no example is known to me in which the central bone is stationary and both end bones are movable. If such cases exist, they are probably rare.) The resultant articular force between the central bone and the distal bone onto which the muscle inserts must be calculated from all the forces, real and fictitious, acting on the distal bone. All these forces can be calculated and placed on the free-body diagram for the distal bone, but they cannot be ascertained from the morphological relationships of the muscle and bones. Once the force at the articulation between the central and distal bones is known, then the free-body diagram for the central bone can be constructed. It should be apparent that for the same two-joint muscle-bone system, the force on the central bone can be quite different, depending on the pattern of forces on the distal bone, even if the muscle force remains constant.

Thus all the functional properties of a two-joint muscle-bone system cannot be determined from only morphological observations; the masses and the moments of inertia of the bones as well as all forces acting on these bones must be known.

2. In general, a pair of one-joint muscles can duplicate the moments produced by a two-joint muscle. However, a pair of one-joint muscles cannot duplicate exactly all the functional properties of a single two-joint muscle; the resultant forces at the articulations would differ, and the

force available for possible linear acceleration of one bone past another would also differ in most cases. The converse to the statement that the torques produced by a two-joint muscle can be duplicated by two one-joint muscles is not true. A single two-joint muscle generally cannot reproduce the moments of a pair of one-joint muscles. Construction of free-body diagrams for a number of examples will readily demonstrate this conclusion.

Elftman (1940, pp. 680–682), in his analysis of the work done by sets of one-joint and of two-joint muscles in human locomotion, assumed that a single two-joint muscle can reproduce the torques of two one-joint muscles. He based his discussion on a system for illustrating torques by arcs of circles the centers of which were at the center of rotation and the radii of which were proportional to the torques. Any muscle force of the same magnitude that is tangential to this arc will produce the same torque. However, Elftman went far beyond this scheme by stating that the force vectors can be applied to the arcs, using them as pulleys, which is not possible because the arcs do not represent morphological structures. Moreover, if the two-joint muscle is tangential to these arcs, then it must develop the tension of one of the one-joint muscles at one end and the tension of the other one-joint muscle at the other end, as was strongly implied by Elftman (1940, p. 681), which, again, is not possible, because the tension of the muscle is the same throughout the length of the two-joint muscle. Moreover, the method of indicating relative magnitudes of torques by arcs is not very useful, because the same torque can be achieved by varying both the moment arm and the force. The use of a system that holds one or both of these factors constant is of limited value.

No doubt exists about the validity of Elftman's general conclusion (1940) that two-joint muscles allow a saving of energy compared to one-joint muscles. However, I cannot agree with his theoretical analysis or with his conclusion on how much energy two-joint muscles save. Elftman stated (1940, p. 681) that the rate at which a two-joint muscle works (the horsepower of the muscle) is the algebraic sum of the rates (one of which may be negative) of the one-joint muscles it replaces; the saving would be the duplication avoided by the two-joint muscle. This amount is probably the maximum possible saving, and most likely the saving of energy of a two-joint muscle would be less, and probably considerably less, than this amount.

3. The torque produced by a two-joint muscle on each bone onto which it attaches is not determined simply by the length of the moment arm from the center of rotation of each bone as has often been assumed (e.g., Elftman, 1941, p. 197; his lever arm is the same as the moment

arm). Calculation of the torque of the two-joint muscle on this basis is correct only when the central bone of the three bone series is stationary and the two outer bones are moving. In most cases, the bone from which the two-joint muscle originates is the stationary bone in the system.

The torque of a two-joint muscle on the distal bone of the series (the bone on which it inserts) depends on the force of the muscle and the moment arm of this vector from the center of rotation of the distal bone. However, the torque on the central bone depends on the resultant force of the distal bone on the central bone and the moment arm of this force from the center of rotation of the second bone. Thus, as shown above, the torque on the central bone cannot be ascertained until the magnitude and direction of the articular force between the distal and proximal bones are known.

4. Two-joint muscles exert the same tension at both points of attachment, as has been stressed by Basmajian (1957, and 1962, p. 68), Manter (1938), and others (a two-joint muscle does not produce equal but oppositely directed torques on the two bones onto which it attaches, as implied by Elftman, 1941, p. 196, although a one-joint muscle does place equal torques on the two bones). The two-joint muscle cannot exert an effect on one attachment without affecting the other, nor could the muscle produce tension and shorten at one end and receive tension and lengthen at the other end, unless it was constructed and attached in a most peculiar way. No two-joint muscle has been described, to my knowledge, with the necessary properties needed for these actions.

Little doubt exists that two-joint muscles possess certain advantages over one-joint muscles, as may be concluded from their common occurrence in all groups of vertebrates. Some of these advantages may stem from the following properties of two-joint muscles.

1. Two-joint muscles exert an effect (produce torques and rectilinear forces) on two moving bones, but one-joint muscles can affect only one moving bone for the same (approximately) amount of energy expended during contraction. Many two-joint muscles are so arranged in the body that their effect on both moving bones is a desirable one for the required movement of the bones. Thus, with two-joint muscles, fewer muscles would be required and less energy would be expended (as stressed by Elftman, 1941, and others) to accomplish the same results.

2. Two-joint muscles, because of their arrangement in the bone-lever system, generally have longer moment arms than do one-joint muscles and therefore need develop less force to produce the same torque. Or, the two-joint muscle could develop a larger torque and therefore impart a greater acceleration on the bone.

3. The greater length of two-joint muscles as compared with that of one-joint muscles may be an advantage in isotonic contractions. Longer muscles shorten with greater speed than do shorter muscles of the same physiological cross section (i.e., muscles that develop the same maximum isotonic tension). Moreover, longer muscles can shorten with less loss of tension and can accelerate bones with less expenditure of energy (see Fenn, 1938, pp. 167–169; and Elftman, 1941, pp. 204–208).

4. The two-joint muscle can transmit tension between the end bones of the three bone series more efficiently (less expenditure of energy) than can the corresponding sets of one-joint muscles, as noted by Elftman (1940, p. 681, and 1941, pp. 204–208). In many places in the body, a ligament cannot connect two bones because of the required movement of the bones. A muscle must be present in such sites to transmit tension. In each such case, the muscle must contract and develop a tension equal to the amount being transmitted. When a single two-joint muscle exists, only one muscle contracts, but, when two one-joint muscles exist, both muscles must contract; hence they use more energy. The efficiency of the two-joint muscle is far greater than the set of one-joint muscles; however, the saving is probably less than half the energy, as might be concluded.

Two-joint muscles do have some disadvantages when compared with one-joint muscles. The major disadvantage of two-joint muscles is that they lack independent control over the distribution of forces about each articulation and over the movement of each bone. Whenever the muscle contracts and develops a certain tension, the movements of the bones and the forces will depend on the whole system and upon all forces acting on it. The effect of the muscle on the individual bones cannot be varied independently. Moreover, the two-joint muscle-bone system is inherently non-static, so that a two-joint muscle by itself could not serve as a holding muscle for static conditions.

Little can be said at this time about the general advantages and disadvantages of two-joint muscles. Detailed theoretical analyses and empirical observations of the functional properties of many different two-joint muscles are needed before general conclusions are possible. On the basis of the above analysis, it seems reasonable to conclude that two-joint muscles may possess an over-all advantage over one-joint muscles except in their lack of ability for independent control at each joint and their unstableness as holding muscles. Hence, it may be suggested that, in a large functional system, such as a limb or the vertebral column or the jaw apparatus, many of the muscles are two-joint muscles, with only enough one-joint muscles about each articulation to provide the necessary independent control of action about each joint and the necessary stability.

FREE-BODY DIAGRAMS: The functional properties of the tensions developed by the contraction of a muscle in its normal position in a bone-muscle system can be analyzed by the application of free-body diagrams. These diagrams have their greatest advantage in their simplicity and in their widespread applicability to almost all, if not all, bone-muscle systems. The only equations needed in free-body diagrams (the sums of the moments and of the vector forces) are simple additive algebraic equations. If all the terms, save one, in each equation are known, then the equations can be solved. Herein lies a major shortcoming of the method in that all but one of the terms must be known. In the analysis of actual cases, it may be difficult or impossible to ascertain all the needed information with the available observational and experimental techniques.

Additional forces acting on the system can be treated readily with the inclusion of an additional term to each equation for each new force. The inclusion of new forces does not increase the complexity of the equation. The only result of a large number of forces in any analysis is that the equations become long and may be rather messy in appearance.

One essential factor in the use of free-body diagrams is the construction of accurate diagrams showing the disposition of all the forces acting on the system. Because of the theoretical approach used in this study, no care was taken to draw the length of the force vectors proportional to the magnitude of the forces. In studies of actual cases, it is recommended that the force vectors be drawn proportional to the size of the force whenever possible. If such is not done, the fact should be stated clearly. A separate diagram should be drawn for each free-body, as was done in figures 2 and 9, after the free-bodies are clearly identified.

Free-body diagrams may be used for both static conditions and dynamic ones in which the bones are being accelerated or decelerated. Static conditions are the easiest to treat. Dynamic conditions are most easily handled when the system is considered as a series of instantaneous conditions. Dynamic conditions may also be analyzed by writing the equations for the changing parameters (such as length of moment arms, size of forces, and so on) and integrating over the required range.

The equations that describe the forces acting on a bone in free-body diagrams present a major stumbling block in dynamic cases, because most of the terms are non-linear. As the bone rotates, the muscle changes in length; hence its force changes according to the tension-length relationships, a curve that cannot be described simply. Moreover, the length of the moment arm of each force changes as well as the angle of intersect between the force vector and the established x and y axes. Writing the equations may be simple enough, but integrating them over the angular

displacement of the bone becomes very difficult. Several simplifying assumptions may have to be used if the equations are integrated. The gain in accuracy obtained in exact solutions may be slight over that obtained by dividing the angle of rotation into a small number of segments and treating each segment as an elongated "instantaneous" acceleration so that the dynamic conditions can be considered as a series of "static" conditions. The solution will not be exact, but it may be close to degree of experimental error involved when the forces, moment arms, angles, and other figures that must be substituted into the equations are being obtained.

Because of these reasons, I believe, and agree with Dempster (1961), that the method of free-body diagrams is a most powerful and useful method of analyzing the functional properties of the force developed by a muscle in its bone-lever system and that this approach has a very widespread applicability in vertebrate (and some invertebrate) functional morphology. Free-body diagrams are, however, not the only method or the most useful one for all applications. Nevertheless, it is clear that a general adoption of free-body diagrams would lead to a far better understanding of the biomechanical properties of muscles in their normal bone-lever systems, and of the adaptive significances of the evolutionary changes of both components of vertebrate bone-muscle systems.

SUMMARY

The mechanics of one-joint and two-joint muscles are described by means of free-body diagrams. Both static and dynamic (rotational and linear motions) conditions are analyzed. Free-body diagrams treat all the forces acting on bodies and allow analysis of the consequences of these forces; the associated equations are simple summations. D'Alembert's principle is employed (inclusion of a fictitious force or torque) in examples of linear or angular acceleration so that the forces and torques are reduced to an equilibrium and can be treated by the method of statics. Centripetal and tangential forces are included whenever a bone is rotating. Equations are written for each example of one-joint and two-joint muscles. A general three-dimensional model is presented.

The use of the notion of first-, second-, and third-class levers is discouraged, because such a classification of lever systems is more misleading than useful.

The mechanics of "spurt" and "shunt" muscles are analyzed, with special emphasis on the amount of torque produced and the contribution to the needed centripetal and tangential forces. "Shunt" muscles could produce as much torque as could "spurt" muscles; the needed centripetal

force may be less than that supplied by the muscles or could be provided by ligaments at the articulation. It is argued that this division of muscles is misleading and even erroneous, and that these terms should be avoided.

The contraction of a muscle does not produce a force couple on each bone onto which the muscle attaches, as has been advocated in the earlier literature. The force at the articulation depends on all other forces, real and fictitious, acting on the bone and, except by rare chance, is not equal in magnitude, parallel, and opposite in direction to the muscle force.

Two-joint muscle-bone systems are non-static (and non-stable if static) and are indeterminate (the consequences of the muscle force cannot be ascertained merely from a knowledge of the morphology). No simple correlation exists between the relationship of the force vector of the muscle to the longitudinal axis of the central bone and the direction of rotation of the central bone. Some of the advantages and disadvantages of two-joint muscles as compared with one-joint muscles are discussed. A completely satisfactory analysis of these advantages and disadvantages must wait until empirical studies of many two-joint muscle-bone systems have been made.

The advantages and disadvantages of free-body diagrams in biomechanical studies are outlined, with the recommendation that all analyses of bone-muscle systems should use free-body diagrams or methods that are clearly derived from free-body diagrams. The strength of such a method is that all the forces acting on each free-body (bone) are included and the consequences of their combined actions can be readily ascertained.

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